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Habitat-specific production rate estimates from 5 Canadian Shield lakes

Estimations du taux de production spécifique à l'habitat pour 5 lacs du Bouclier canadien

T.C. Pratt

Fisheries and Oceans Canada
Great Lakes Laboratory for Fisheries and Aquatic Sciences
1 Canal Drive
Sault Ste Marie, ON, P6A 6W4

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ABSTRACT

Estimating habitat-specific production rates is a difficult but crucial component of meeting Fisheries and Oceans Canada's policy of 'no net loss of productive capacity of fish habitats' as outlined in the *Fisheries Act*. In this study, an underwater visual technique was used to estimate habitat-specific littoral zone fish densities. Passive traps were concurrently fished in each habitat type, and the weight of captured fish was used, in combination with the available density estimates and estimates of habitat availability, to provide habitat-specific biomass estimates for each species. These estimates were converted into habitat-specific production estimates in one of two ways; by multiplying habitat-specific biomass estimates with published species-specific production:biomass ratios to determine habitat production indices (HPI), and by estimating actual habitat-specific production rates by conducting visual censuses and biomass estimates over two time periods. The underwater visual method for determining habitat-specific densities was validated by conducting a concurrent mark-recapture population estimate in the five study lakes. The visual abundance estimates successfully predicted 75% of the variation in the mark-recapture population estimates, indicating that the underwater visual method is capable of providing habitat-specific density, biomass and production estimates. Structurally complex habitats contained the highest fish densities and biomass, and provided the greatest potential for production. Given the high cost and variability observed in habitat-specific production rate estimates, the use of underwater visual methods for determining habitat-specific density estimates, in combination with published production:biomass ratios, provides the simplest and most effective method for estimating habitat-specific production.

RÉSUMÉ

L'estimation du taux de production par habitat est une tâche difficile, mais essentielle, pour respecter la politique de Pêches et Océans Canada d'« aucune perte nette » de la capacité de production des habitats du poisson énoncée dans la *Loi sur les pêches*. Dans le cadre de la présente étude, on a utilisé une technique visuelle sous-marine pour évaluer la densité de poissons par habitat d'une zone littorale. Des pièges passifs ont été pêchés simultanément dans chaque type d'habitat. On a utilisé le poids des poissons capturés, combiné aux estimations de la densité disponibles et aux estimations des habitats disponibles, pour obtenir des estimations de la biomasse par habitat pour chaque espèce. Ces estimations ont été converties en estimations de la production par habitat de deux façons : en multipliant les estimations de la biomasse par habitat par les rapports production:biomasse par espèce publiés afin de calculer les indices de production de l'habitat, et en estimant le taux de production par habitat réel grâce à des recensements visuels et des estimations de la biomasse pendant deux périodes. La méthode visuelle sous-marine employée pour déterminer la densité par habitat a été validée en effectuant une estimation de la population par marquage et recapture simultanément dans les cinq lacs à l'étude. Grâce aux estimations visuelles de l'abondance, on a pu prédire 75 % de la variation des estimations de la population par marquage-recapture, ce qui montre que la méthode visuelle sous-marine peut fournir des estimations de la densité, de la biomasse et de la production par habitat. La densité et la biomasse de poissons les plus élevées ont été observées dans les habitats de structure complexe. Ces habitats présentaient le plus grand potentiel de production. Étant donné le coût élevé et la variabilité des estimations du taux de production par habitat, l'utilisation de méthodes visuelles sous-marines pour obtenir des estimations de la densité par habitat, combinée aux rapports production:biomasse publiés, constitue la méthode la plus simple et la plus efficace d'estimer la production par habitat.

INTRODUCTION

Estimating habitat-specific production rates (the amount of fish flesh added per unit time (Ricker 1975)) is a challenging but crucial component of meeting Fisheries and Oceans Canada's policy of 'no net loss of productive capacity of fish habitats' as outlined in the *Fisheries Act* (DFO 1986). Habitat managers face site-level decisions about development proposals, and if developments that result in harmful alterations, disruptions or destruction to fish habitat are authorized, managers must agree to a compensation plan. Determining what is lost to development, versus what is gained by the proposed compensation, requires habitat-specific estimates of fish production.

Fish habitat use is dependent on a complex interaction of physiological requirements (e.g. temperature, oxygen, ambient light levels) (Ryder 1977, Christie and Regier 1988) and biological interactions, including food availability and predation risk (Werner et al. 1983). High habitat heterogeneity is thought to be critical for maintaining fish production (Weaver et al. 1996), as structurally complex habitats provide refuge areas for juvenile fishes and more surface area for primary and secondary production to occur (Rozas and Odum 1988). The quantification of habitat use, and converting habitat utilization patterns into habitat-specific production estimates, is seldom achieved (Randall 2003).

In this study, I used an underwater transect technique to determine habitat-specific fish densities for nearshore areas < 2 m in depth, which, when used in combination with known habitat areas and biomass data from captured individuals over two time periods, ultimately provided habitat-specific production rates from five small Canadian Shield lakes.

METHODS

Study area

Four of the lakes used in this study are located in the Turkey Lakes Watershed (TLW), a long-term acid-rain monitoring research watershed located on the Canadian Shield in the Algoma district of Ontario, Canada. An entire issue of the Canadian Journal of Fisheries and Aquatic Sciences (Volume 45, Supplement 1) is devoted to the history of research in the TLW. The fifth lake, Quinn Lake, is located approximately 55 km south-east of the other lakes. All five lakes are small, nutrient poor, have good visibility and contain relatively depauperate fish communities (Table 1).

Underwater visual protocol validation

Densities for each fish species and life stage were estimated by habitat type in early (June and early July) and late (August) summer 2003 following the general procedures outlined in Buckland et al. (1993). The number of days between assessments (and thus the length of time available for production) varied slightly for each lake; Lower Batchawana (46 days) had the shortest time between visits, while Upper Batchawana and Quinn (55 days) had the longest. Five habitat types were selected after pilot projects on these lakes in 2001, based on simple physical features, including substrate type and cover (Table 2). Limited macrophyte growth in these nutrient-poor lakes meant that fallen trees provided much of the littoral zone structure, so both wood and beaver lodge were included as habitat

types in this study. A single assessment was performed using the same methodology in 2002, allowing for the determination of habitat-specific fish densities but not production.

A transect constructed of gill net lead-line was laid perpendicular to shore, beginning at the 2 m depth contour. Transects were 30 m in length (marked every m), and had 2 m crosspieces (marked at 5 cm intervals) located every 5 m. Transects were snorkelled by swimming slowly towards shore, with habitat type, fish species, life stage and perpendicular distance (in relation to the centre transect line) noted on wrist slates for each fish sighting. A number of habitat types could therefore be present on a single transect. When fish were aggregated (which they commonly were), habitat type, aggregation size and composition, and the perpendicular distance of the centre of the aggregation were noted.

Transects were carried out until an acceptable coefficient of variation, a measure of variance in the data, was reached for abundance estimates from each habitat type. This meant that the initial 30 transect locations were randomized, but specific habitat types were targeted after the initial transects to improve precision around abundance estimates. This typically resulted in rarer habitats being sampled in higher proportion than their availability (Table 3).

Randall (2003) stated that habitat-based surrogates of productive capacity must be validated, preferably on a whole-system scale (Level II validation, Randall 2003). The five lakes involved in this production study were also part of a whole-system habitat perturbation study, for which whole-lake mark-recapture estimates were collected for each species on an annual basis from 1998-2003. In 2002-03, fish were collected in a variety of gear (baited minnow traps, hoop nets, and trap nets) and marked with a fin clip. For all species, a Chapman-adjusted Schnabel estimate,

$$N' = \frac{\sum C_t M_t}{(R' + 1.92)}$$

where C_t = # captured, M_t = # marked, and R' = # recaptured, was calculated.

Density, biomass and production estimates

Habitat-specific perpendicular sighting distances collected while snorkelling were entered into the DISTANCE software package (Thomas et al. 2002), where species and life stage-specific sighting probability curves were calculated and ultimately habitat-specific density estimates determined. The five lakes used in this study were also used for a geographic information system-based habitat determination study (Frezza 2001), so estimates of habitat area were available for each lake (Table 2). Density estimates were multiplied by habitat area to provide habitat-specific abundance estimates.

In all lakes, baited minnow traps were fished in each of the five habitat types concurrent with the underwater transects. Captured fish were weighed (g) on-site and released. 50 fish of each species and life stage were targeted from each habitat type. These habitat-specific species and life stage biomass estimates were calculated for both the early and late summer snorkelling periods. Biomass estimates were summed across species to provide habitat-specific biomass estimates.

Habitat-specific summer production rates were determined by first calculating instantaneous population growth rate from the early and late summer visual abundance estimates (G_x, Ricker 1975) for each life stage of every species where habitat-specific

abundance estimates were available from the two sampling periods, and then estimating the production of each life stage by $P_x = B_x \times G_x$ (Ricker 1975). Separation into life stages was based on simple size determination (e.g. age-0 or adult). Production rates were then summed across life stages within habitat types to provide habitat-specific summer production rates.

Habitat-specific production, as estimated by the habitat productivity index (HPI), was also calculated using production per unit biomass (*P/B*) ratios (Downing and Plante 1993, Randall and Minns 2000). The HPI is calculated by summing the product of habitat-specific biomass and the associated *P/B* ratio for each species for each habitat type.

Statistical analyses

A simple linear regression model was constructed to determine how well visual abundance estimates were able to predict mark-recapture population estimates. Data from 2002 and 2003 were natural log +1 transformed to meet normality assumptions. A multiple regression model was used on the data to determine whether adding Secchi depth, a measure of observer detectability, improved the regression fit.

Habitat-specific density and biomass estimates for all species and life stages observed were ln (density + 1) transformed to meet normality assumptions, and the resulting values used in a two-way analysis of variance (with habitat type and time period as factors) to test for differences in fish habitat use and fish biomass. Time was considered as a factor in the above analysis as it was apparent that many fish had spawned in the duration between the early and late sampling period, resulting in an increased number of life stages available for analysis. When significant among-habitat differences were detected, Tukey honest-significant difference (HSD) post-hoc tests were employed to separate habitat types. The above data were also used to calculate a habitat-specific density and biomass coefficient of variation (coefficient of variation = standard deviation / mean) for each time period to determine which habitats were more variable in the fish habitat use and biomass patterns.

Habitat-specific summer production rate estimates were tested for among-habitat differences using a nonparametric Kruskal-Wallis one-way analysis of variance, as the data could not be normalized. One data point, from Quinn beaver lodge habitat, was an outlier and not used in the above analysis. HPI data were ln (x+1) transformed to meet normality assumptions, and tested for among-habitat differences in a one-way analysis of variance. HPI values from the two time periods were averaged to provide a single HPI value from each habitat for each lake. Tukey HSD post-hoc tests were employed to separate habitat types. The two estimates of production, production rate and HPI, were compared by Pearson-product correlation analysis to determine if there was concordance between estimates from each habitat in each lake.

RESULTS

Underwater visual protocol validation

Whole-lake Schnabel and underwater visual population estimates were obtained for 19 populations, 9 in 2002 and 10 in 2003, across the five study lakes (Table 4). A simple linear regression showed that mark-recapture abundance estimates were significantly

positively related to visual abundance estimates (ln (mark-recapture estimate +1) = 2.38 + 0.69 (ln (visual estimate + 1)); $r^2 = 0.74$; $P = <0.001$; Figure 1). Visual estimates tended to be larger than mark-recapture estimates for large population sizes, and smaller at smaller sizes. Adding Secchi depth to create a multiple regression model slightly improved the explanatory power (ln (mark-recapture estimate +1) = 0.94 + 0.73 (ln (visual estimate + 1) + 0.24 (Secchi depth); $r^2 = 0.80$; $P = <0.001$), but only the visual estimate was a significant predictor of the mark-recapture estimate (visual estimate $P = <0.001$; Secchi depth $P = 0.06$).

Density, biomass and production estimates

Significant differences in fish densities were found among habitats ($F_{4,195} = 7.7$; $P = <0.001$) and between time periods ($F_{1,195} = 23.2$; $P = <0.001$), but the habitat-by-time interaction was not significant ($F_{4,195} = 0.9$; $P = 0.45$) (Figure 2a). Beaver lodges contained significantly higher densities of fish than all other habitat types, and vegetated sites contained higher densities of fish than open sites. No additional among-habitat differences were detected. Significantly more fish were observed during the late sampling period (August) than the early sampling period (June/July) in all habitat types.

Habitat use was more variable in all habitat types during the early sampling period (Figure 2b). In particular, open and wood habitats displayed high variability in fish habitat use. Variability in habitat use dropped greatly for all habitats except rock substrate habitats during the late sampling period, and wood habitats went from having the highest coefficient of variation in the early period to the lowest in the late period.

Habitat-specific biomass followed a similar pattern to the density data. Significant differences in fish biomass were found among habitats ($F_{4,40} = 14.8$; $P = <0.001$) and between time periods ($F_{1,40} = 23.9$; $P = <0.001$), but the habitat-by-time interaction was not significant ($F_{4,40} = 2.5$; $P = 0.17$) (Figure 3a). Beaver lodges contained significantly higher area-specific biomass than all other habitat types, while wood habitats had significantly higher biomass than open habitats. No other among-habitat differences were significant. Biomass was greater in the late sampling period than the early sampling period in all habitat types.

Habitat-specific biomass was more variable in the early sampling period in all habitats except beaver lodges (Figure 3b). Variability in habitat-specific biomass was particularly high in open, rock and wood habitats in the early sampling period, and it remained high in open and rock habitats in the late sampling period.

Habitat-specific production was highly variable among lakes, and no among habitat differences were found ($H_4 = 1.8$; $P = 0.77$) (Figure 4a). Interestingly, negative production was observed in six habitats; three wood, two beaver lodge and one rock habitat, across four of the lakes. The HPI differed significantly among habitats ($F_{4,20} = 9.9$; $P = 0.0001$) (Figure 4b). HPI patterns mirrored biomass trends, with beaver lodges containing significantly higher HPI values than all other habitat types except wood, and wood habitats having significantly higher HPI values than open habitats. No other among-habitat differences were significant. Habitat-specific production rates were significantly correlated with HPI values ($r = 0.43$, $P = 0.042$; (Figure 5).

DISCUSSION

Underwater visual protocol validation

One successful outcome of this research was the validation of habitat-based visual population estimates against traditional whole-lake mark-recapture population estimates. Randall (2003) emphasized the importance of what he termed level II validation, the comparison of habitat-based estimates with whole-population estimates, when using habitat-based surrogates of fish production. The ability of the visual abundance estimates to account for 75 percent of the variance in mark-recapture estimates, given the inherent limitations of the visual method as discussed below, implies that the underwater visual census technique can provide reasonable abundance estimates by habitat type, at least for the species censused in these five lakes. The development of a technique capable of successfully demarcating heavily utilized from less important habitat types is important for the delivery of Fisheries and Oceans Canada Habitat Management Program.

The underwater visual technique outlined in this manuscript only surveyed depths ≤ 2 m, which may explain the tendency for the under-representation of some species in the visual estimates. While many species use shallow water as a refuge from predation and thus may be adequately censused in depths ≤ 2 m (Schlosser 1988, Angermeier 1992, Pratt and Fox 2001), other species surveyed in this study undoubtedly also use deeper littoral areas. This would account for the consistently lower population estimates of white sucker detected by the visual technique, as white suckers are readily captured at depths outside of the study boundaries (Scott and Crossman 1973). Underwater visual census techniques have consistent biases, including differences in observer delectability between cryptic and transient-pelagic species, and different sizes or life stages of the same species (Brock 1982). However, none of the species involved in the validation component of this research would be classified as either behaviourally cryptic or transient-pelagic, and larger individuals were rarely censused. Thus, the primary reason that the whole-lake and habitat-specific estimates would not concur, given the species involved, should be the limited depth coverage of the visual technique. This limitation could be easily addressed, though, as the entire littoral zone could be censused with the underwater visual technique using divers instead of snorkellers.

An explanation for the tendency of the visual technique to overestimate abundances of high density populations and populations from poor visibility systems likely resides in the calculation of the DISTANCE detection function. The detection function assumes absolute detection at the transects' center, with a broad shoulder of high detection to a given distance from the centerline, followed by a rapid decrease in detection past that distance (Buckland et al. 1993). The overestimation of high density populations likely results from observers underestimating the perpendicular sighting distance of the center of fish aggregations (Kulbicki and Sarramega 1999). This would move the observations into an area of higher probability of detection, and somewhat inflate the resulting population estimates.

Including Secchi depth in the visual and mark-recapture estimate regression model improved its' explanatory power, indicating that visual estimates are influenced by observer visibility. In low visibility systems, few observations occur in the area of rapid decline, resulting in almost all data arising from areas with a high probability of detection.

The inclusion of all data may artificially broaden the area of high detection, leading to an overestimation of abundance. Truncation to remove data points from the low detection areas may shift the shape of the detection function and lower abundance estimates; preliminary re-analyses of the Wishart Lake show lower abundance estimates using a 1 m truncation distance.

Density, biomass and production estimates

This research was less successful in clearly identifying production rate differences among the five pre-defined habitat types. Randall (2003) noted that actual fish production is rarely measured due to high cost, and that surrogates for production are typically used instead. In this study, both approaches were used, but only the HPI (a surrogate technique) was able to differentiate among habitat types. Habitat-specific production rates were highly variable among lakes, except for production from open habitats which was uniformly low. As HPI values were correlated with production rates, it is apparent that surrogates such as the HPI could be favoured over actual production rate estimates as they are less variable and less expensive to obtain. HPI estimates were validated against literature estimates of production (Randall and Minns 2000), but this is the first ever validation of HPI in the field.

While the overall production from each lake was positive, negative production was observed in six of the twenty-five habitats sampled. Negative production, caused by a loss in mean fish weight over time, has been detected in other populations over the winter (Kelso and Ward 1972) and during periods of intense competition (Jones et al. 1977). In this study, negative production typically occurred in habitats that had high densities of ripe females in the first sampling period. The second assessment occurred post-spawning, resulting in negative growth, and ultimately negative production, from that habitat. Given that most production occurs in age-0 fish (Jones et al. 1977), and that in this study age-0 fish were more randomly distributed across habitats than adults, it seems possible that the occurrence of negative growth for specific habitat types favoured by spawners could be widespread. At the very least, this phenomenon should be looked for in other systems.

Beaver lodges clearly supported higher densities, area-specific biomass, and production (as measure by HPI) than the other habitats, but no other significant patterns emerged. Fish habitat use is usually related to the structural complexity of a given habitat type (e.g. Werner et al. 1977, Rozas and Odum 1988), and beaver lodges were clearly the most complex habitat in this study. Beaver lodges have a high surface area for primary and secondary production, contain diverse macroinvertebrate (Rolauffs et al. 2001) and fish communities (France 1997) despite their limited spatial coverage. Patterns in abundance, biomass and production were apparent among the remaining habitats, as open habitats were always less favoured, but high variability limited the detection of differences. Rock substrate, vegetation and wood habitats all contain some level of structural complexity, while open habitats had none. While aquatic macrophytes are the primary source of structure and the main habitat used by fish in more eutrophic lakes (Werner et al. 1977, Weaver et al. 1996, Pratt and Smokorowski 2003), aquatic vegetation in more nutrient poor lakes is generally less structurally complex. The dominant macrophyte in the study lakes was pipewort (*Eriocaulon aquaticum*), a grass-like perennial found in oligotrophic, soft-water lakes (Fassett 1969). Thus, it is possible that rock, vegetation and wood habitats are functionally similar in these lakes, which would account for their apparent approximately

equal importance. To date, researchers have only been successful in discriminating 2 or 3 habitat types, based on the presence or absence of cover (Randall et al. 1998, Pratt and Smokorowski 2003); a similar pattern may exist in these study lakes (e.g. beaver lodge = high cover, rock, wood and vegetation = medium cover, open = no cover).

An important assumption with the habitat-based production rate estimates calculated herein is whether there is significant movement among habitats. If fish primarily reside and feed in the same habitat type, the approach outlined in this manuscript has shown itself to be a potentially important technique for determining habitat-specific production estimates. However, if fish habitat use is more ephemeral and fish production can be attributed to habitats other than where individuals were observed, a scale-mismatch occurs and the relationship between habitat and fish production breaks down (Randall 2003). A preliminary habitat-specific mark-recapture trial in one of the production study lakes, where fish were captured in a particular habitat, marked with a habitat-specific mark, and then released in all five habitat types, found that 75% of all recaptures were within the original habitat, despite only 32% of all releases occurring in those habitats (T. Pratt, unpublished data). Habitat fidelity is seen in some species (e.g. striped bass (*Morone saxatilis*) (Jackson and Hightower 2001, Young and Isely 2002), but a more rigorous assessment of this assumption is needed in future years.

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Table 1. Physical and biological characteristics of the five production study lakes.

Lake	Surface area (ha)	Mean depth (m)	July Secchi depth (m)	July total phosphorus (mg/L)	Fish species present[a]
Upper Batchawana	5.9	3.9	4.8	0.005	FSD, BKT
Lower Batchawana	5.8	3.2	4.2	0.006	FSD, BKT
Wishart	19.2	2.2	2.6	0.007	LKC, EMS, SPS, NRD, FHM, WHS, BKT, BRB
Little Turkey	21.0	6.0	5.2	0.007	LKC, GDS, EMS, SPS, NRD, FHM, WHS, BKT, LKT, BRB, NSS, LGP
Quinn	6.9	2.7	3.8	0.016	GDS, NRD, BKT

[a] Species abbreviations, common names and scientific names: LKC = lake chub *Couesius plumbeus*; GDS = golden shiner *Notemigonus crysoleucas*; EMS = emerald shiner *Notropis atherinoides*; SPS = spottail shiner *Notropis hudsonius*; NRD = northern redbelly dace *Phoxinus eos*; FSD = finescale dace *Phoxinus neogaeus*; FHM = fathead minnow *Pimephales promelas*; WHS = white sucker *Catostomus commersoni*; BKT = brook trout *Salvelinus fontinalis*; LKT = lake trout *Salvelinus namaycush*; BRB = burbot; NSS = ninespine stickleback *Pungitius pungitius*; LGP = logperch *Percina caprodes*

Table 2. Littoral zone (<2 m depth) habitat availability, by lake, for the five production study lakes.

Lake	Habitat Class				
	Open (ha)	Rock (ha)	Vegetation (ha)	Wood (ha)	Beaver Lodge (ha)
Upper Batchawana	0.68	0.12	2.24	0.07	0.01
Lower Batchawana	0.62	0.17	1.91	0.03	0.01
Wishart	4.94	2.67	3.19	0.06	0.01
Little Turkey	2.00	0.81	1.41	0.12	0.01
Quinn	0.89	0.05	1.10	0.11	0.01

Table 3. Transect effort and habitat area sampled by lake for the five production study lakes.

Lake	Habitat Class					Total area sampled (m^2)	Number of transects
	Open (m^2)	Rock (m^2)	Veg (m^2)	Wood (m^2)	Beaver (m^2)		
Upper Batchawana	379.75	43.25	707.5	10.0	47.75	1188.25	57
Lower Batchawana	328.25	42.0	699.0	8.75	64.0	1142.0	65
Wishart	456.75	373.25	88.75	22.75	41.25	982.75	66
Little Turkey	478.75	289.75	143.75	38.5	46	996.75	67
Quinn	649.5	16.5	482.5	142.5	26	1317.0	86

Table 4. A comparison of whole-lake Chapman-adjusted Schnabel mark-recapture and underwater visual transect population estimates for adult fish from the five production study lakes. Only species where both techniques provided an estimate are displayed here. Values in brackets represent 95% confidence intervals.

Lake	Species[a]	Year	Abundance Estimates	
			Mark-recapture (95% confidence interval)	Visual (95% confidence interval)
Upper Batchawana	FSD	2002	6145 (4082-9179)	2852 (1389-5855)
		2003	2073 (1389-3073)	625 (152-2755)
Lower Batchawana	FSD	2002	2142 (640-3731)	4148 (2331-7382)
		2003	2118 (1200-3630)	1586 (565-4457)
	BKT	2002	485 (214-955)	623 (248-1670)
		2003	369 (198-660)	439 (204-943)
Wishart	NRD	2002	2013 (1887-2148)	8143 (4202-15780)
		2003	3683 (3456-3925)	21410 (8524-53774)
	WHS	2002	1319 (764-2219)	741 (182-3022)
Little Turkey	NRD	2002	10969 (10097-11916)	17054 (8005-36333)
		2003	6658 (6364-6966)	10039 (6746-14938)
	FHM	2003	209 (135-321)	202 (21-1915)
	WHS	2003	280 (124-553)	94 (40-222)
	LGP	2002	5424 (1957-10669)	1747 (1130-2701)
		2003	1562 (941-2547)	1849 (1224-2794)
Quinn	GDS	2002	11135 (7786-15857)	13758 (3878-48808)
		2003	5032 (4660-5435)	3291 (1604-6574)
	NRD	2002	8632 (7962-9358)	7484 (4546-12319)
		2003	6319 (6103-6543)	7819 (4210-14520)

[a] Species abbreviations and fish common names and scientific names are found at the bottom of Table 1

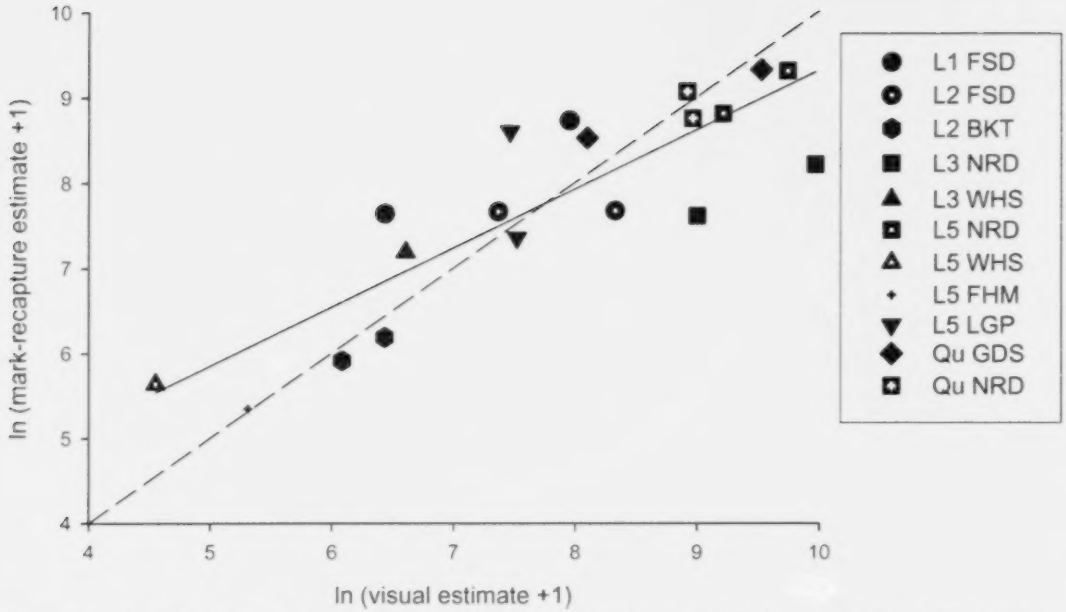

Figure 1. Simple linear regression between visual and mark-recapture abundance estimates from five lakes over two years of concurrent visual and mark-recapture data collection. The solid line represents the best fit linear regression, while the dotted line is the 1:1 line. Species abbreviations are located in Table 1.

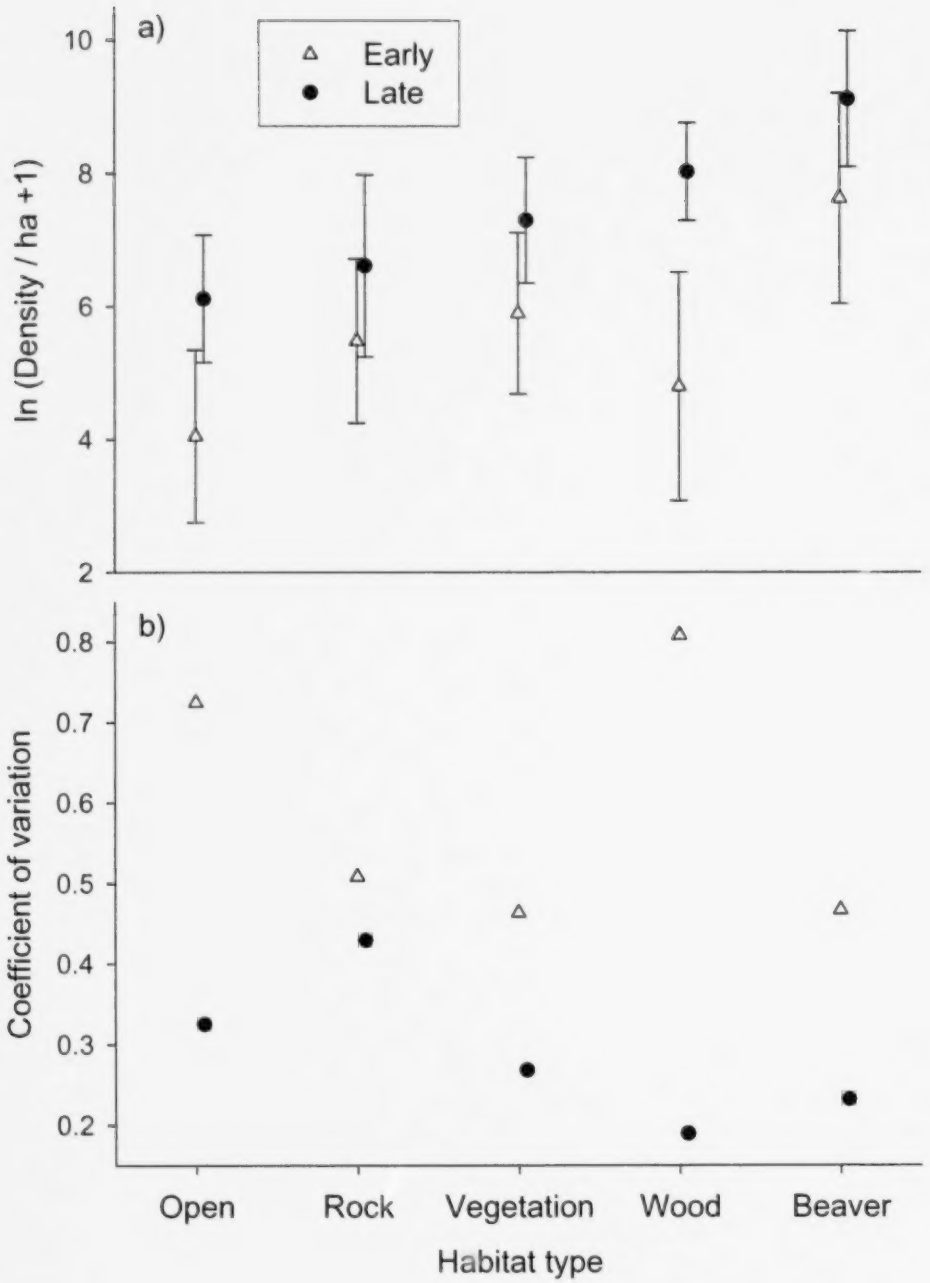

Figure 2. a) Mean habitat-specific fish densities across two time periods (early and late summer) from five Canadian Shield lakes. Error bars represent 95% confidence intervals. b) A measure of variation in habitat-specific fish densities across two time periods in the five production study lakes.

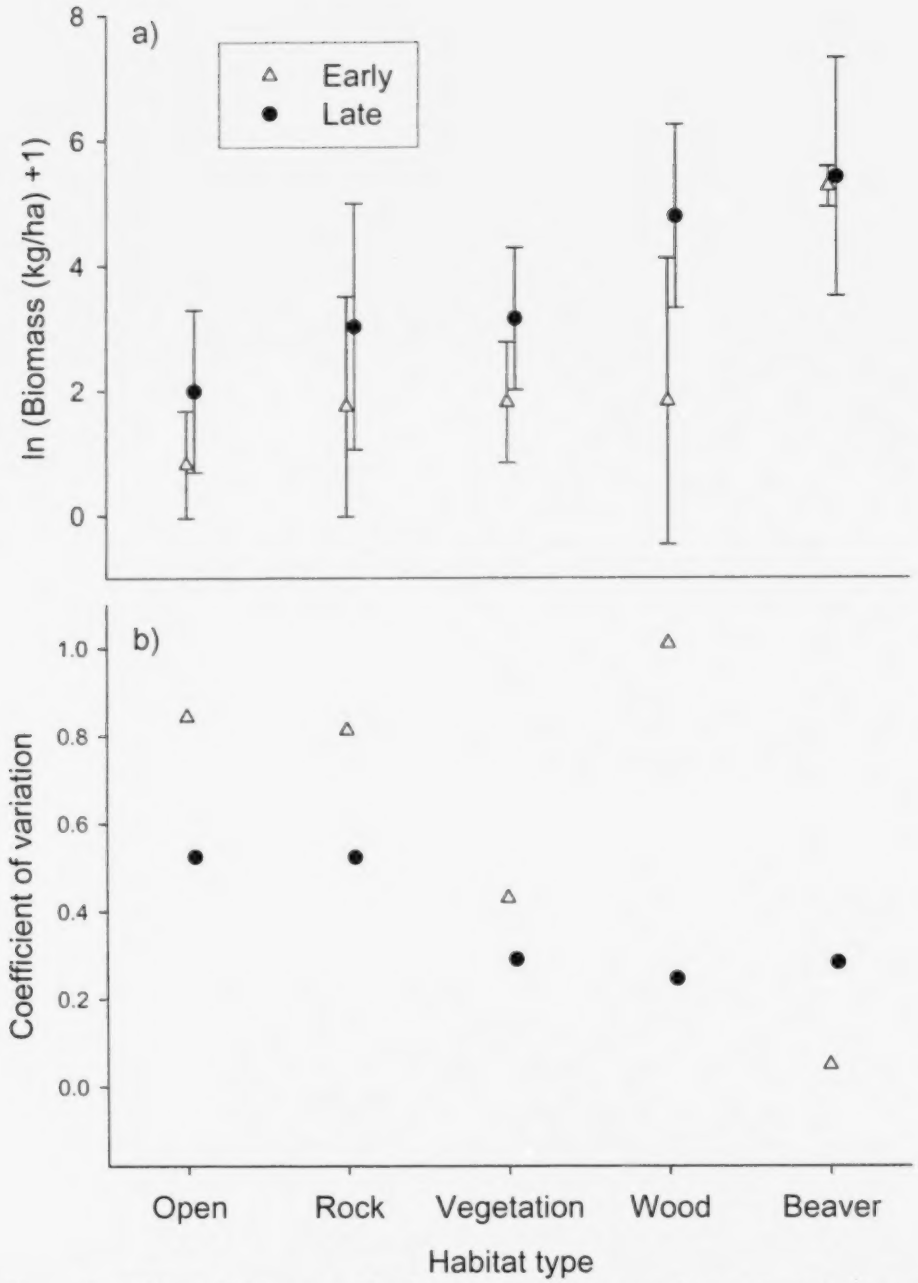

Figure 3. a) Mean habitat-specific fish biomass from two time periods (early and late summer) in five Canadian Shield lakes. Error bars represent 95% confidence intervals. b) A measure of variation in habitat-specific fish biomass across two time periods in the five production study lakes.

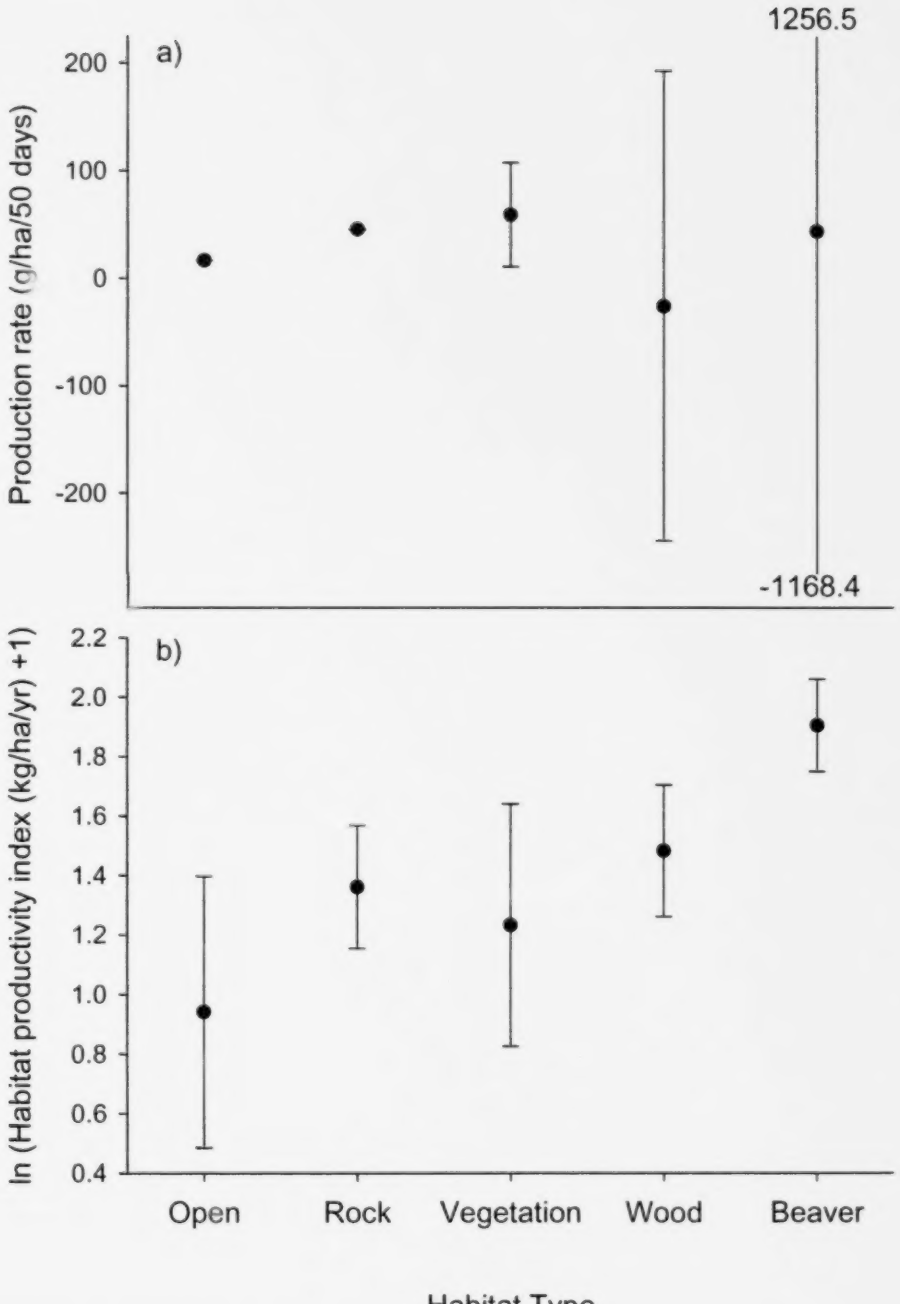

Figure 4. a) Habitat-specific production rate, over a 50 day period in mid-summer, by habitat type from five Canadian Shield lakes. Error bars represent 95% confidence intervals. b) Mean habitat productivity index (HPI) of five habitat types. Error bars represent 95% confidence intervals.

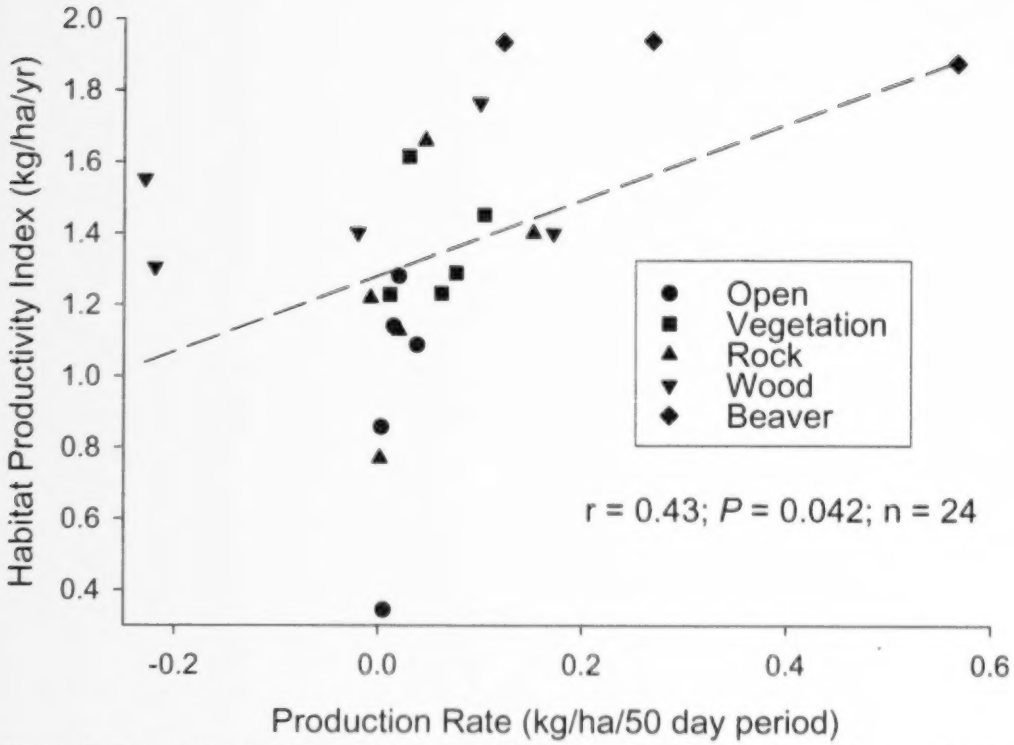

Figure 5. Correlation between habitat-specific production rate and the habitat production index (HPI) from five habitat types in the five production study lakes.